

which they had to contend against, we may judge an individual by its external appearance in the last resort only; we determine its systematic position far rather from its internal organization, as displayed to us by means of anatomy and histology, and above all from its embryology.

The latter lead us to the conclusion that Nemertines have probably been derived from Turbellarian-like forms, but that after following a line of development over which the Annelids had already passed, they diverged from it again in a direction of their own.

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XLVIII.—*On the Fate of the Quadrate in Mammals.*

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ONE of the most troublesome points in the study of the descent of the Mammalia is the explanation of the changes which have taken place in the structure of the lower jaw and in its mode of articulation with the skull. In Amphibians and Reptiles the lower jaw is invariably made up of a number of pieces and articulates with the skull by means of the quadrate. In Mammals the jaw is apparently a single bone articulating with the squamosal. What we have therefore to explain is, What has become of the quadrate and how has the jaw become simplified? In the present paper I shall only deal with the fate of the quadrate.

Hitherto the majority of comparative anatomists, chiefly from the study of the early condition of the visceral arches, have agreed in finding the homologue of the quadrate in one or other of the auditory ossicles. Gegenbaur, Kölliker, Wiedersheim, and Reichert find its representative in the incus, while Huxley looks upon the malleus as its equivalent. Parker, who has done more than any one else to elucidate the development of the skull, after for many years holding the same view as Huxley, ultimately came to regard the incus as the Mammalian quadrate.

That the quadrate of the Amphibian or Reptilian ancestors of the Mammals should gradually move back from the articulation of the jaw and degenerate into one of the auditory ossicles is improbable; and there is little doubt but that the view has been founded on a misinterpretation of the morpho-

logical value of the malleus and incus. The researches of Peters \*, Dollo †, Baur ‡, and Gadow § place it beyond doubt that the Mammalian auditory ossicles are together homologous with the Reptilian columella auris and extra-columella, and that the malleus and incus can never have taken any part in the articulation of the jaw.

An entirely different view of the fate of the quadrate has recently been revived by Albrecht ||, and has been supported by Dollo, Cope ¶, and Baur. According to this view the quadrate is represented by the zygomatic portion of the squamosal. It is highly probable that the Mammalian squamosal represents more than one element; but the palæontological evidence which would find in it the quadrate is unsatisfactory, the zygomatic portion being most probably homologous with the quadrato-jugal.

Gadow and Seeley \*\* advocate the view of Cuvier and Owen, that the quadrate is represented by the tympanic bone. This, however, involves a gradual shifting back of the quadrate from the articulation, which, though conceivable, is not borne out by positive evidence either from palæontology, embryology, or comparative anatomy.

The Mammalia and Reptilia seem to have had a common origin in a group of highly developed Amphibians, of which no remains have as yet come to light, but of which *Pareiasaurus* is the nearest ally as yet known. In these ancestral forms there was in all probability but a feebly developed flattened quadrate, probably ossified and articulating with the quadrato-jugal, squamosal, and pterygoid. In *Pareiasaurus* Seeley †† says the quadrate bone "would appear to have been

\* W. Peters, "Ueber die Gehörknöchelchen und ihre Verhältniss zu den ersten Zungenbogen bei *Sphenodon punctatus*," Monatsber. d. k. preuss. Akad. d. Wiss., Berlin, 1874.

† L. Dollo, "On the Malleus of the Lacertilia, &c.," Quart. Journ. Micr. Sc. 1883.

‡ G. Baur, "On the Quadrate in the Mammalia," Quart. Journ. Micr. Sc. 1887.

§ H. Gadow, "On the Modifications of the First and Second Visceral Arches, &c.," Phil. Trans. vol. clxxix, 1888.

|| P. Albrecht, 'Sur la valeur morphologique de l'articulation mandibulaire, &c.,' Bruxelles, 1883.

¶ E. D. Cope, "The Relations between the Theromorphous Reptiles and the Monotreme Mammalia," Proc. Amer. Assoc. Adv. Sci. vol. xxxiii. 1884.

\*\* H. G. Seeley, "On the Anomodont Reptilia and their Allies," Phil. Trans. vol. clxxx., 1889.

†† H. G. Seeley, "On *Pareiasaurus bombidens* (Owen), and the Significance of its Affinities to Amphibians, Reptiles, and Mammals," Phil. Trans. vol. clxxix., 1888.

a very short flattened bone with a ball-like articular surface on the palatal aspect of the head."

In the Reptilian branch of descendants the quadrate gradually became more powerfully developed to give a firmer articulation to a snapping jaw. Still, in the primitive reptiles we find the quadrate but feebly developed. In *Dicynodon* we find it as a comparatively small bone so feebly articulated with the descending process of the squamosal and the pterygoid that it is lost from many of the British Museum specimens. Even in *Ichthyosaurus*, which is well advanced along the Reptilian line, we still find a small quadrate.

In the Mammalian line of descent, with the development of flexible muscular lips and cheeks a looser articulation of the jaw became advantageous. The short flattened quadrate with the rounded articular surface was doubtless gradually transformed into a flattened bony plate, giving great freedom of movement to the condyle of the jaw. In process of time nature found an equally firm and more elastic medium of articulation in an ossified quadrate, which remains in the Mammals of to-day as the *Interarticular Cartilage*.

The condition of affairs in the skull of a monstrosity I recently described\* would seem to favour this view as against the other theories advanced. In this specimen there is no trace of a lower jaw, and the only part of the first visceral arch to be detected is an irregular piece of bone about half the size of the malleus, representing the fused palatines and pterygoids. The zygomatic portion of the squamosal, though altered in shape somewhat, is unusually well developed, while the tympanics are present as a powerful arch of bone stretching from one side of the skull to the other. It is difficult to believe that either squamosal or tympanic can represent part of an arch whose development is in its other parts so completely arrested.

Should the present theory be confirmed by further research, the Interarticular Cartilage might appropriately be called the "Quadrate Cartilage."

\* "On the Condition of the Auditory Ossicles of a Synotic Cyclopiian Lamb," Trans. Nat. Hist. Soc. Glasg. 1888-89.